# SYSTEMATICS OF MIRABILIS SUBGENUS QUAMOCLIDION (NYCTAGINACEAE)

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Monographs and revisions by Standley (1909, 1911, 1918) and Heimerl (1889, 1897, 1934) form the basis of the present taxonomic knowledge of a predominantly North American family. After having studied the family for over two decades, Standley (1931a) stated that he knew few groups of plants in which specific differences were more unstable or baffling. After studying South American material, Standley (1931b) transferred to *Mirabilis* all those plants he had previously placed in *Oxybaphus, Hesperonia, Quamoclidion,* and *Allioniella*. Heimerl (1934) followed Standley's circumscription of *Mirabilis* but retained *Quamoclidion* with the single species of *Q. triflorum*. Subsequent treatments of *Mirabilis* (sensu Standley, 1931b) have dealt only with small parts of the genus as they are represented in regional floras.

Plants referable to *Mirabilis* subgenus *Quamoclidion* are characterized by a gamophyllous involucre that is only slightly accrescent after anthesis and surrounds three or more flowers. An initial purpose of this study was to compare the broad, ovate, distinct bract subtending each individual flower of *Hermidium alipes* with the gamophyllous involucre of *Quamoclidion*. As a taxonomic result of this study I am transferring *Hermidium alipes* to *Mirabilis* subgenus *Quamoclidion*.

Mirabilis subgenus Quamoclidion comprises six species that grow predominantly in western North America between  $20^{\circ}-45^{\circ}$  N. Open habitats at the lowermost edge of juniper woodland are where most populations and the greatest number of plants per population are found. Quamoclidion is not restricted, however, to areas where Juniperus occurs. Milabilis triftora inhabits a scrub vegetation dominated by Acacia, Opuntia, and an occasional Ficus in Baja California del Sur and in Jalisco. At the other geographic extreme M. marfarlanei shares dry sand bars with Celtis on the floors of the Snake and Salmon River canyons.

## MORPHOLOGY

My circumscription of *Quamoclidion* is based on characters that are stable and rather uniform within the subgenus but which differ widely in other members of Nyctaginaceae. These include inflorescence and pollen morphologies as well as chromosome number and habitat preference. Floral and fruit morphologies possess the most diagnostic characters for circumscription of species within *Quamoclidion* because they are stable at the population level but may vary considerably within a species. Leaf

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shape and vestiture vary considerably even within populations. Unfortunately, characters used by other authors (Heimerl, 1934; Standley, 1918) to delimit species of *Mirabilis* are those which I have found to vary widely within populations due to extreme seasonally and environmentally induced morphological variation.

INFLORESCENCE. Flowers of Quamoclidion are arranged in solitary, determinate, involucrate heads at ends of branches and in axils of upper cauline leaves. As in *Bougainvillea*, each flower is intimately associated with a subtending bract. Most taxa of Quamoclidion have a sixflowered head consisting of a naked, solitary, central flower surrounded by five flowers borne on the bases of gamophyllous involucral bracts. Occasionally the central flower is not naked. In all taxa of *Quamoclidion*, I have observed heads that possess central flowers subtended by a distinct bract similar to one of the involucral bracts. Barneby (1942) stated that this occasional occurrence suggests that heads of "advanced" members of *Quamoclidion* may have evolved rather recently from the "primitive bougainvilleoid" flower head of Mirabilis alipes, in which every flower has its own independent, subtending floral bract. Although distinct bracts are usual in this species, heads with the five outermost bracts united by their margins to one-half their length are common. These involucres are campanulate and have the aspect of the gamophyllous involucres of other taxa within Ouamoclidion.

Exceptions to the six-flowered head of most taxa of *Quamoclidion* occur in the consistently three-flowered *Mirabilis triftora* and in *M. greenei* with as many as 16 flowers in some involucres. When a second or third whorl of flowers is present, each member of the whorl is borne on the midvein of one of the five bracts, each one distal to the flower of the first whorl. Flowers on the second and third whorls often abort before anthesis but many others may produce fruit.

POLLEN. Nowicke (1970), utilizing light microscope and scanning electron microscope techniques, found that pollen of Nyctaginaceae is structurally variable; however, features within genera are remarkably uniform. This is certainly true for the uniformly very large, spheroidal, and pantoporate pollen grains, with a spinulose sexine pattern, of *Quamoclidion*. Pollen-grain diameters form a continuum (100–160  $\mu$ m) and are not taxonomically useful for separating taxa within the subgenus. The range, standard deviation, and mean of pollen-grain diameters from 54 collections of *Quamoclidion* may be found elsewhere (Pilz, 1974).

Pollen viability is typically very high. If immature flowers or flowers from plants that are obviously under water stress are observed, the pollen viability sometimes drops below 90%. The relatively small pollengrain diameter reported by Nowicke (1970) for *Mirabilis alipes* is probably due to the selection of an immature flower. A notable exception, *M. pudica*, often has 30-50% of its grains ill-formed and noticeably smaller than the mean grain size of other species. These smaller grains also fail to stain in aniline blue-lactophenol. Only one collection of *M. pudica* (*Beatley 8211*, RSA) has nearly 100% viable pollen, and this is coupled with a significantly smaller grain diameter than is typical of the species. This aspect of the reproductive biology of *M. pudica* requires further study because other collections made by Beatley in the same area have the low viability typically found in the species throughout its geographic range.

FRUITS. The basal portion of the perianth begins to enlarge rapidly soon after fertilization, reaching a size slightly larger than that of the mature fruit. It is initially bright green and contains an ovary that is about one-fifth that of the ultimate size of the fruit. The developing embryo enlarges and fills the cavity of the persistent perianth, and the mature fruit is termed an anthocarp: "a fruit formed by the union of floral organs or part of them, with the fruit itself" (Jackson, 1928). A thin pericarp envelops the single uncinate embryo and the mealy perisperm. The endosperm is completely absorbed during growth and maturation of the embryo, except for a small amount forming a cap or collar around the apex of the radicle. Cells of the nucellus become packed with starch and form a mealy perisperm, which constitutes the storage tissue of the mature seed (Cooper, 1949).

Anthocarps are generally ellipsoidal, although they range from narrowly ovoid to subglobose (Fig. 1). The proximal end is constricted and the distal end may be so to a lesser extent. Anthocarps are brown to nearly black except in *Mirabilis alipes*, which has olive-green fruits that turn brown only if they are wetted after maturity and allowed to dry again. Ten slender, tan, longitudinal ribs are evident on anthocarps of most species, particularly those of *M. multiflora*. These are remnants of vascular traces that earlier extended to the upper portion of the perianth.

The surface of mature anthocarps is sparsely pubescent in Mirabilis triflora and in some individuals of M. multiflora var. glandulosa. Other members of Quamoclidion have glabrous anthocarps. The anthocarp surface is smooth or rugulose, a difference that is correlated with production of mucilage by the fruit when wetted. The rugulose anthocarps of M. triflora, M. alipes, M. greenei, M. macfarlanei, and M. multiflora var. glandulosa produce mucilage in variable amounts. Mirabilis triflora produces a light mucilage that surrounds the fruit and is two or three times the volume of the anthocarp. Other mucilage-formers produce a thick heavy substance that is usually less than 1 mm thick. Plants of those taxa that have smooth anthocarps, on the other hand, produce no mucilage when wetted. Mirabilis pudica, M. multiflora var. multiflora and M. multiflora var. pubescens are included in this second group.

CHROMOSOME NUMBERS AND REPRODUCTIVE BIOLOGY Chromosome numbers have been reported for only 19 of the more than



FIG. 1. Representative flowers and anthocarps of Mirabilis subg. Quamoclidion. Collection numbers are mine unless otherwise indicated. Voucher specimens are in UC. A. M. alipes 788, A'. 1125; B. M. macfarlanei Constance et al. 1579. B'. 1282; C. M., triflora 1270, C'. 949; D. M. pudica Ripley & Barneby 4403, D'. 1132; E. M. greenei 998, E'. 990; F. M. multiflora var. multiflora 1235, F'. 869; G. M. multiflora var. glandulosa 1151, G'. Osterhout 6559; H. M. multiflora var. pubescens 831.

250 taxa of Nyctaginaceae (Pilz, 1974). Many counts were determined from serial sections of paraffin-imbedded material, a technique that can easily lead to errors in interpretation (Epling et al., 1962). Showalter (1935), using paraffin-imbedded material reported n = 29 for *Mirabilis multiflora*. This report is probably due to incorrect interpretation of sectioned material. Using slightly modified aceto-carmine squash techniques (Beeks, 1955; Pilz, 1974) for anthers and root tips I have consistently found the gametic chromosome number n = 33 in the taxa under consideration throughout their geographical ranges (Table 1). This consistency is significant in view of the variation existing within the family as a whole. Species of the same genus within the family tend to have identical chromosome numbers although considerable variation occurs within both *Boerhavia* and *Bougainvillea* that have both aneuploid and polyploid series (Pilz, 1974).

Except for *Mirabilis triflora* all species of *Quamoclidion* are nightblooming. The ephemeral flowers usually open about three hours before dusk and close about mid-morning. Cloudy days may extend the hours that flowers remain open in the morning; however, once closed, the thin delicate perianth lobes become flaccid and do not reopen.

Visitations to flowers by several kinds of animals have been observed, but only hummingbirds and hawkmoths are effective pollinators. Ants, bees, butterflies, and even flies commonly visit the flowers and collect pollen (Cruden, 1970), but the exserted style, 2–30 mm beyond the perianth tube, and its position at one side of the flower make the transfer of pollen to the stigma by these organisms rare.

I have observed *Hylocharis xanthusii*, the Black-Fronted Hummingbird, a species restricted to the southern half of Baja California, to be the principal pollinator of *Mirabilis triflora* in that region. While hovering before the long red tubular flower and taking nectar, the birds brush the exserted stamens and stigma with the tops of their heads, which become yellow with pollen. Hummingbirds show very low species consisten-

 TABLE 1. CHROMOSOME NUMBERS IN Mirabilis SUBG. Quamoclidion. Collection numbers are mine. Voucher specimens are in UC.

- *M. multiflora* (Torr.) Gray var. *multiflora*. New Mexico, Grant Co., 3 mi. W of San Lorenzo, 724, 2n = 33 II. New Mexico, Catron Co., 10 mi S of Luna, 726, 2n = 33 II. Arizona, Coconino Co., 6 mi SE of Desert View, 1236, 2n = 66. New Mexico, Rio Arriba Co., 8 mi W of Abiquiu Dam, 1245, 2n = 66.
- *M. multiflora* (Torr.) Gray var. *pubescens* S. Wats. California, Kern Co., Caliente, 081, 2n = 66. Arizona, Mohave Co., 23 mi E of Kingman, 910, 2n = 33 II. California, Kern Co., Caliente, 961, 2n = 33 II. Nevada, Lincoln Co., 13 mi S of Caliente, 1143, 2n = 33 II.

*M. multiflora* (Torr.) Gray var. *glandulosa* (Standley) Macbr. Nevada, White Pine Co., 1 mi E of Connor's Pass, 1144, 2n = 33 II.

*M. triflora Bentl.* Baja California del Sur, 2 mi N of La Burrera, 947, 2n = 33 II.

*M. pudica* Barneby. Nevada, Lincoln Co., 4 mi W of Crystal Spring, 975 2n = 33 II. *M. greenei* S. Wats. California, Glenn Co., 7 mi N of Stonyford, 1274, 2n = 33 II.

cy when visiting flowers unless a single nectar-producing species markedly predominates (Baker, 1961). *Mirabilis triflora* often grows in large, dense populations in the Laguna Mountains of Baja California del Sur, and this, along with the abundance of hummingbirds observed visiting the flowers, may account for the very high percentage of seed set (see further discussion below).

Pollinators of taxa other than Mirabilis triflora are less certainly known. Baker (1961) reported that M. multiflora var. pubescens (M. froebelii) is visited by hawkmoths, Celerio lineata, at the University of California Botanical Garden in Berkeley, but this site is outside the natural range of the species. He also noted that hummingbirds make their visits in the morning and evening when the flowers are open, and he hypothesized that the sharing of flowers by both hawkmoths and hummingbirds may be a widespread phenomenon (Baker, 1961). Cruden (1973) stated that flower opening and anther dehiscence occurs too late in the day in M. multiflora for visits by hummingbirds and bees "prior to visitation by hawkmoths, the coevolved pollinators". In contrast, I have observed hummingbirds and hawkmoths sharing flowers of M. multiflora with dehisced anthers at dusk in Grant County, New Mexico. Thus at least some sharing of floral resources by these two pollinators is occurring late in the day soon after the flowers open. No pollinators of other taxa have been reported, and I have not observed any.

The amount of seed set on a plant is often extremely low. Plants isolated from others by more than 100 m rarely produce fruit. This probably is due to their self-incompatible breeding system, known in at least three taxa (Pilz, 1974), coupled with the lack of compatible pollen transfer to these isolated plants. Many populations fail to produce fruit in a given year. I have recorded abortion, presumably due to lack of available water, of all flower buds on all plants of some populations of *Mirabilis alipes*, *M. macfarlanei*, *M. greenei*, and *M. multiflora*. Absence of pollinator visits during periods of strong winds also contributes to low seed set recorded for populations of *M. alipes*.

Establishment of new plants within a population is presumably infrequent in this group of long-lived perennials. In three years of field work I have seen only two first-year seedlings. After the first-year stage it is difficut if not impossible to estimate the age of plants, so I have little idea of the age-distribution of plants within populations.

## TAXONOMIC TREATMENT

MIRABILIS L. subg. QUAMOCLIDION (Choisy) Jepson, Flora Calif. 1(4):457. 1974. — Quamoclidion Choisy in DC. Prodr. 13(2):429.
1849. — Mirabilis sect. Quamoclidion (Choisy) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859 [This combination has been erroneously attributed to Heimerl, Nat. Pflanzenfam. 3(1b):24. 1889]. Type: Mirabilis triflora Benth. Hermidium S. Wats., Bot. King's Exped. 5:286. 1871. Type: Hermidium alipes S. Wats.

Mirabilis sect. Paramirabilis Heimerl, Notizbl. Bot. Gart. Berlin-Dahlem 11(106):453. 1932. Type: Heimerl (1932) included two species in this section; I here designate as lectotype, Mirabilis multiflora (Torr.) Gray.

Herbaceous perennials from a long spongy cylindrical taproot, the stems branching alternately or subdichotomously from an expanded multicipital caudex; branches erect or ascending to nearly decumbent, the primary branches stout, more slender above, swollen at nodes; herbage green, occasionally purplish-red on surfaces exposed to direct sunlight, densely pubescent to glabrous; leave opposite, petiolate, thin to succulent, decurrent at base onto petiole, margins entire to repand; lowermost leaves orbicular to widely ovate; middle cauline leaves very widely ovate to ovate; uppermost leaves ovate to lanceolate, highly reduced near involucre; leaf stomata anomocytic; peduncles axillary and in terminal cymes, erect to abruptly reflexed; flowers involucrate, heads 3–16-flowered: involucral bracts connate to distinct, slightly accrescent in age; perianth tubular, campanulate, or funnelform-salverform, magenta to creamy white, constricted above the ovary, the limb 5-lobed; stamens 5, circinate before anthesis, filaments unequal, capillary, pubescent to glabrous, connate at base into a cup enveloping the ovary; anther of paired locules, yellow, versatile, loculicidal; pollen grains spheroidal, pantoporate, sexine spinulose, spinules 1  $\mu$ m long; ovary ellipsoidal, green, style filiform, glabrous, stigma capitate, papillose, magenta; anthocarp ovoid to ellipsoidal, smooth to rugulose, glabrous to sparsely pubescent; seed with light brown testa, adherent to pericarp; embryo uncinate, perisperm enclosed on three sides by cotyledons and bounded by hypocotyl and descending radicle on the other. Chromosome number n = 33.

Involucrate heads 5–16-flowered; involucral bracts 12–35 mm long; fruit 5–11 mm long.

Free portion of perianth campanulate.

- 1. MIRABILIS ALIPES (S. Wats.) Pilz, comb. nov.—Hermidium alipes S. Wats., Bot. King's Exped. 5:268. 1871. Type: Nevada, Humboldt Valley, May 1868, S. Watson 968 (erroneously cited as "1860" and "960" by Standley, 1909). Holotype: US! isotypes; GH!, NY!
- Hermidium alipes S. Wats. var. pallidium Porter, Rhodora 54:158. 1952. Type: Utah, Uintah Co., "on the Wasatch formation, 5 miles south of Vernal", 3 June 1950, C. L. Porter 5308. Holotype: RM!; isotypes: CAS!, MO!, RSA!, SMU!, TEX!, UC!

Plants from taproot 1-2 m long, 3-5 cm in diameter; branches erect or ascending to nearly decumbent, 2-4 dm high, forming hemispheric clumps 6-8 dm in diameter, the primary branches stout, 4-6 mm thick, more slender above: herbage pale green, glabrous to very sparsely puberulent: leaves horizontally spreading, succulent, glaucescent: lowermost leaves suborbicular to widely ovate and occasionally asymmetrical, 4-7 cm long, 3.5-6.5 cm wide, base rounded, apex obtuse to rounded and occasionally apiculate; middle cauline leaves ovate to widely ovate and often asymmetrical, 4.5-5.0(-9) cm long, 3.5-4.0(-5) cm wide, base rounded, apex obtuse (rarely acute) and occasionally apiculate; uppermost leaves narrowly ovate and symmetrical, 2.5-4.0 cm long, 1-2 cm wide, base obtuse to rounded, apex acute; petioles often narrowly winged, 5-7 mm long on lower leaves, the uppermost leaves subsessile; leaf stomata 30-36 µm long, 18-24 µm wide: peduncles 3-10 mm long, 1 mm in diameter, erect to ascending; involucre consisting of distinct bracts, or bracts united by their margins to one-half their length, the tube to 15 mm long or lacking and the free portions 15-30 mm long, 10-25 mm wide, ovate, apex acute to obtuse (rarely rounded), often apiculate; involucre 6-8(-9)-flowered, the individual flowers borne on pedicels 0.2-1.0 mm long on midvein of involucral bract, 1 flower on each midvein; perianth campanulate, 15-16 mm long, magenta, occasionally creamy white, glabrous, tube 6-7 mm long, 5-6 mm broad, throat gradually widening, 5-6 mm long, the 5 lobes very widely ovate, 1-2 mm long, 7-10 mm broad, apex emarginate, longitudinal nerves 5, extending to the sinus, apex of nerve pubescent; stamens equalling perianth, filaments pubescent to middle, glabrous above, pollen grains 106-133 µm in diameter; style exserted 2-10 mm; anthocarp ellipsoidal with 10 slender tan longitudinal ribs, slightly constricted at both proximal and distal ends, 5.5-7.0 mm long, 3.0-4.5 m wide, mottled olive-green, rugulose, glabrous, producing a thick heavy mucilage when wetted.

DISTRIBUTION (Fig. 2). Scattered throughout much of Great Basin; transmontane California (Inyo and Mono counties) across Nevada and Utah to Rio Blanco Co., Colorado. On gravelly-sandy soil of mesas, washes, and alluvial fans between 1200 and 2000 m in Shadscale Scrub and Sagebrush Scrub, or, rarely, Pinyon-Juniper Woodland. Flowers early May through mid-June.



FIG. 2. Distribution and date of collection of Mirabilis,

The status of *Mirabilis alipes* as a monotypic representative of a distinct genus, *Hermidium*, has always been based on the possession of discrete involucral bracts (Heimerl, 1934; Standley, 1918). Although perfectly distinct bracts are typical, heads with the five outermost bracts united by their margins to one-half their length are common. These involucres are campanulate and have the aspect of the gamophyllous involucres of other taxa within *Quamoclidion*. Flowers, leaves, and fruits of *M. alipes* closely resemble those of other taxa within *Quamoclidion*. Much more morphological variation occurs within *Mirabilis* (sensu Standley, 1931b) than exists between *Quamoclidion* and *Hermidium*. Thus the inclusion of *M. alipes* within subgenus *Quamoclidion* places it with its closest relatives and represents the most "natural" classification for these species.

I have observed several populations of plants in Pershing, Washoe, and Nye counties, Nevada (*Pilz 1113, 1127, 1128, 1276–79;* all in UC), which possess creamy white perianths and are referrable to Porter's (1952) var. *pallidum* from northeastern Utah. These occur, in this region, in populations with plants possessing purple perianths and a wide range of intermediate colors. They do not appear distinct enough to warrant varietal status.

MIRABILIS PUDICA Barneby, Leafl. W. Bot. 3:175. 1942. Type: Barneby (1942) designated two cotypes; I here designate as lectotype (CAS!): Nevada, Lincoln Co., "3 miles W. of Crystal Springs", 10 May 1942, *Ripley and Barneby 4403*. Isotypes: GH!, K!, NY!, RSA!, UC!

Plants from a taproot 1-2 m long, 3-5 cm in diameter; branches erect or ascending, 3-5(-6) dm high, forming upright columnar clumps 3-5dm in diameter, the primary branches 3-5 mm thick, more slender above; herbage pale green to whitish, glabrous to densely pubescent; leaves conspicuously ascending, very often vertically oriented, succulent, glaucescent; lowermost leaves ovate to widely ovate and symmetrical, 1.5-3.0 cm long, 1.0-2.5 cm wide, base obtuse to acute, apex acute to rounded and apiculate; middle cauline leaves ovate to narrowly ovate and symmetrical, 3.5-5.0 cm long, 2.0-2.5 cm wide, base acute to rounded (rarely cordate), apex acute; uppermost leaves narrowly ovate to lanceolate and symmetrical, 1.4-3.7 cm long, 0.5-1.8 cm wide, base rounded to acute, apex acute; petioles short, often narrowly winged, 3-5 mm long on lowermost leaves, the uppermost leaves subsessile; leaf stomata 27-36 µm long, 24-30 µm wide; peduncles 6-10 mm long, 1 mm in diameter, abruptly reflexed to produce a pendent involucre; involucre campanulate to nearly rotate in fruit, 12-21 mm long, the bracts united by their margins, the tube 5-10 mm long, unequally 5-lobed, free portion of bract 6-12 mm long, 9-17 mm wide at base, triangular to widely ovate, apex acute, apiculate; involucre 6-flowered, the flowers borne on pedicels 0.2-1.0 mm long, on midvein of involucral bracts, 1 flower on each midvein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth campanulate, 12–14 mm long, creamy white, glabrous to densely pubescent, the tube 5–6 mm long, 6–7 mm broad, the throat gradually widening, 5–6 mm long, the five lobes very widely ovate, 2–3 mm long, 6–9 mm broad, apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exserted 2–4 mm, filaments villous to middle, glabrous above, pollen grains 110–145  $\mu$ m in diameter; style exserted 3–5 mm; anthocarp ellipsoidal to widely ellipsoidal with 10 slender tan ribs occasionally evident at base, occasionally constricted at both proximal and distal ends, 7–8 mm long, 4.5–5.0 mm wide, dark brown, smooth, glabrous, not producing mucilage when wetted.

DISTRIBUTION (Fig. 2). On calcareous alkaline hills and sandy playas of Lincoln and Nye counties, Nevada, in Shadscale Scrub and Creosote Bush Scrub between 1000 and 1500 m. Flowers early May to mid-June.

This is a distinctive species within *Quamoclidion* because of its heads, which are pendent upon recurved peduncles, and its conspicuously ascending, often vertically oriented, leaves.

3. MIRABILIS MACFARLANEI Constance & Rollins, Proc. Biol. Soc. Wash. 49:148. 1936. Type: Oregon, Wallowa Co., "Lower Cottonwood Landing, between mouth of Somer's Creek and Pittsburg Landing, Snake River Canyon", 15 May 1936, *Constance, Rollins, Clements and Dillon 1579*. Holotype: WS!; isotypes: CAS!, DS-2 sheets!, GH!, JEPS!, K!, MO!, NY!, POM-2 sheets!, RM!, UC-2 sheets!, US-2 sheets!, WIS!, WS!

Plants from taproot 1-2 m long, 3-5 cm in diameter; branches erect or ascending to nearly decumbent, 6-8(-10) dm high, forming hemispheric clumps 8-10(-12) dm in diameter, the primary branches stout, 6-8 mm thick, more slender above; herbage green, glabrous to sparsely puberulent; leaves horizontally spreading, succulent, glaucescent on lower surface; lowermost leaves orbicular to very widely ovate, 2.0-5.5 cm long, 2.5-6.5 cm wide, base obtuse to cordate and often asymmetrical, apex rounded to broadly obtuse (rarely short apiculate); middle cauline leaves suborbicular to widely ovate, 3.5-4.5 cm long, 3.0-4.5 cm wide, base obtuse to cordate and symmetrical, apex obtuse to rounded (rarely acute) and often short apiculate; uppermost leaves ovate and symmetrical, 1.5-3.0 cm long, 1.0-2.5 cm wide, base rounded to obtuse (rarely cordate), apex acute; petioles stout, 17-25 mm long on lowermost leaves, the uppermost leaves subsessile; leaf stomata 27–30  $\mu$ m long, 21–24  $\mu$ m wide, peduncles 4-8(-25) mm long, 1 mm in diameter, erect to ascending; involucre campanulate to nearly rotate in fruit, 13-20 mm long, the bracts united by their margins, the tube 6-12 mm long, unequally 5lobed, the free portion of bract 6-12 mm long, 11-14 mm wide at base, triangular to very widely ovate, the apex acute to acuminate; involucre 6-flowered, the flowers borne on pedicels 1-3 mm long, on midvein of

involucral bracts, 1 flower on each midvein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnelformsalverform, 15–25 mm long, magenta, glabrous, the tube 7–12 mm long, 3–4 mm broad, the throat gradually widening, 5–7 mm long, the five lobes very widely ovate, 2–3 mm long, 6–9 mm broad, the apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exserted 3–4 mm, filaments glabrous, pollen grains 115–122 $\mu$ m in diameter; style exserted 4–5 mm; anthocarp ellipsoidal with 10 slender tan ribs, constricted at the proximal and often the distal end, 6–7 mm long, 3–4 mm wide, brown to dark brown, slightly tuberculate, glabrous, mucilaginous when wetted.

DISTRIBUTION (Fig. 2). On dry exposed slopes bordering the Snake and Salmon rivers of Oregon and Idaho, between 450 and 500 m. Flowers throughout May.

*Mirabilis macjarlanei* is most notable for its geographic isolation in the Snake and Salmon river canyons. These are much more arid than the surrounding canyon walls and mountain slopes, which support Yellow Pine Forest. The closest relative of this species is probably *Mirabilis multiflora* var. *glandulosa* with which it shares a funnelform-salverform perianth, general anthocarp characteristics, and a similar though more depauperate flavonoid profile (Pilz, 1974).

This taxon is named for E. B. MacFarlane, for 30 years a pilot of boats on the Snake River, who pointed out the location of the plant to the authors. It has been said that Harold St. John had pointed out the plant to MacFarlane on an earlier trip up the river, but St. John did not publish his find (Constance, pers. comm.).

4. MIRABILIS GREENEI S. Wats., Proc. Amer. Acad. Arts 12:253. 1876 (1877). — Quamoclidion greenei (S. Wats.) Standley, Contr. U. S. Natl. Herb. 12:358. 1909. Type: California, Siskiyou Co., "mountain sides about Yreka", 20 June 1876, E. L. Greene 876. Holotype: GH! mounted with V. Rattan 56, June 1884; isotype: NY! mounted with T. Howell 1389, July 1889.

Plants from taproot 2–4 m long, 3-5(-12) cm in diameter; branches erect or ascending to nearly decumbent, 4–8 dm high, forming hemispheric clumps 6–10 dm in diameter, the primary branches stout, 5–13 mm thick, more slender above; herbage green, glabrous to very sparsely puberulent; leaves horizontally spreading, succulent, glaucescent; lowermost leaves orbicular to suborbicular, 3.0-5.5 cm long, 2.5-5.0 cm wide, base obtuse to cordate and often asymmetrical, apex rounded to obtuse; middle cauline leaves widely elliptic to ovate, 4.0-7.5 cm long, 3.0-4.5cm wide, base obtuse and often asymmetrical, apex acute or acuminate; uppermost leaves narrowly ovate to elliptic and symmetrical, 2.7-4.5 cm long, 1.0-2.5 cm wide, acute at base and apex; petioles stout, 10-27 mm long on lowermost leaves, the uppermost leaves subsessile; leaf stomata  $30-36 \ \mu m \ long$ ,  $24-30 \ \mu m \ wide$ ; peduncles  $25-85 \ mm \ long$ ,  $1.5-2.0 \ mm$ 

### PILZ: MIRABILIS

in diameter, erect or ascending; involucre campanulate, 26-36 mm long, the bracts united by their margins, the tube 13–20 mm long, unequally 5-lobed, the free portion of bract 10-17 mm long, 10-13 mm wide at base, triangular to widely ovate, the apex acute to acuminate; involucre 6(-16)-flowered, the flowers borne on pedicels 1–4 mm long, on midvein of involucral bract, as many as 3 flowers borne along a single bract, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnelform-salverform, 40-50 mm long, magenta, glabrous, the tube 25–30 mm long, 5–7 mm broad, the throat gradually widening, 12– 15 mm long, the five lobes very widely ovate, 3-5 mm long, 10-14 mm broad, the apex emarginate, the five longitudinal nerves extending to and 1 mm beyond the sinus, apex of nerve densely pubescent; stamens excerted 1–5 mm, filaments glabrous, pollen grains 130–150  $\mu$ m in diameter; style exserted 3-5 mm; anthocarp widely obovoid to widely ellipsoidal, 5-angulate, constricted at both proximal and distal ends, 7.0-7.5 mm long, 4.0-4.5 mm wide, light brown, tuberculate, very sparsely puberulent to glabrous, mucilaginous when wetted, the mucilage most abundant on ribs (10 visible when wet).

DISTRIBUTION (Fig. 2). Scattered on eastern flank of North Coast and Klamath ranges from Colusa Co. to Siskiyou Co., California. Growing on steep talus slopes and gravelly flats with junipers from 400 to 1000 m. Flowers early May to mid-June.

*Mirabilis greenei* is easily recognizable within *Quamoclidion* because of its distinctive 5-angled fruit, an involucre that often surrounds more than six flowers, and a novel flavonoid profile (Pilz, 1974).

5. MIRABILIS MULTIFLORA (Torr.) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859.

Plants from taproot 1-2 m long, 2-5 cm in diameter; branches erect or ascending to nearly decumbent, forming hemispheric clumps 6-8 dm in diameter, the primary branches stout, 5-12 mm thick, more slender above; herbage green, densely pubescent to glabrous; leaves horizontally spreading, succulent, glaucescent; lowermost leaves orbicular to very widely ovate and often asymmetrical, (3-)5-12 cm long, (4-)5-15 cm wide, base rounded to cordate, apex rounded to obtuse, occasionally mucronate; middle cauline leaves ovate to very widely ovate and often asymmetrical, 5–10 cm long, 4–8 cm wide, base cordate to rounded, apex obtuse to acuminate and often apiculate; uppermost leaves widely ovate to narrowly ovate and only slightly asymmetrical, 2-7 cm long, 1-5 cm wide, base cordate to obtuse, apex acute to acuminate and often apiculate; petioles slender to stout, 20-40 mm long on lowermost leaves, the uppermost leaves subsessile; leaf stomata 24–36  $\mu$ m long, the bracts peduncles 4-75 mm long, 1-2 mm in diameter, erect to ascending; involucre campanulate to broadly campanulate, 22-35 mm long, the bracts united by their margins, the tube 11-25 mm long, unequally 5-lobed, the free portion of bract 6-14 mm long, 8-17 mm wide at base, triangular to

very widely ovate, apex acute to rarely obtuse in fruit, apiculate; involucre 6-flowered, the flowers borne on pedicels up to 2 mm long on midvein of involucral bracts, one flower on each midvein, the central flower solitary and naked (rarely subtended by a distinct bract); perianth funnelform-salverform, 40–60 mm long, magenta, occasionally the tube green, puberulent to glabrous, the tube 27–40 mm long, 5–10 mm broad, the throat gradually widening, 10–20 mm long, the five lobes very widely ovate, 2–7 mm long, 10–20 mm broad, apex emarginate, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exserted 1–10 mm, filaments glabrous to pubescent, pollen grains 118–150  $\mu$ m in diameter; style exserted 3–13 mm; anthocarp ellipsoidal to widely ellipsoidal, often constricted at both proximal and distal ends, 6–11 mm long, 4.0–5.5 mm wide, brown with 10 slender tan longitudinal ribs alternating with 10 raised dark brown (often interrupted) ribs to nearly solid black, rugulose to smooth, glabrous to pubescent, the muci-

lage production diverse.

*Mirabilis multiflora* may be divided into three varieties as follows: Fruit smooth to only slightly tuberculate, producing no mucilage when

wetted; involucral bracts acute.

Fruit dark brown to black, the ribs inconspicuous
5a. M. multiflora var. multiflora.
Fruit light brown with 10 slender tan longitudinal ribs alternating with 10 brown (often interrupted) ribs

Fruit definitely tuberculate, producing mucilage when wetted; involucral

5a. MIRABILIS MULTIFLORA (Torr.) Gray var. MULTIFLORA—Oxybaphus multiflorus Torr., Ann. Lyceum Nat. Hist. New York 2:237. 1827.
— Allionia multiflora (Torr.) Eaton, Man. Bot. ed. 5 Addenda:2.
1829. — Nyctaginia? torreyana Choisy, in DC. Prodr. 13(2):430.
1849, illegitimate superfluous name. — Quamoclidion multiflorum (Torr.) Torr. ex Gray, Amer. J. Sci. Arts II. 15:321. 1853. Type: "Forks of the Platte" (label), "About the Forks of the Platte" (protologue), 1820, Dr. E. James s.n. Holotype:NY!; isotype:K!

DISTRIBUTION (Fig. 3). Occasional in Chihuahua, Coahuila, Nuevo Leon, and San Luis Potosi, Mexico. More often collected in western Texas, through New Mexico, Arizona, and Colorado, United States of America. On gravelly-sandy or loose soils of mesas, washes, and open hillsides between 300 and 2300 m in Pinyon-Juniper Woodland and Yellow Pine Forest. Flowers mid-May through mid-October.

Among the plants collected by Edwin James, M.D., Assistant Surgeon in the United States Army, in the summer of 1820, was a member of Nyctaginaceae collected "About the Forks of the Platte" (Torrey, 1827). The specimen is incomplete and Torrey (1827) stated that the "country was traversed with great rapidity..., and little opportunity was afforded of making observations, or even of recording all the stations of the plants." This collection was published as Oxybaphus multiflorus by Torrey. After crossing the Platte River at Forks (now Lincoln County, Nebraska, fide McKelvey, 1955) the party, commanded by Major Stephen H. Long, continued up the South Platte River to the base of the Rocky Mountains. I have not seen plants belonging to Torrey's O. multiflorus from Nebraska. The closest locality lies over 400 km southwest in Pueblo County, Colorado. Given Torrey's remark that James' records were not always complete, it seems probable that the collection of O. multiflorus was made later in James' journey, perhaps somewhere on the eastern flank of the Rocky Mountains where the plants are known to occur.

5b. MIRABILIS MULTIFLORA (Torr.) Gray var. PUBESCENS S. Wats., Bot. Calif. 2:2. 1880, Type: In the protologue Watson stated, "The variety is peculiar to S. California, from near Fort Tejon (Wallace, Kennedy) to San Diego County, Palmer." Of the three collections cited by Watson only Wallace's is at the Grav Herbarium (GH), and it consists solely of two detached involucres and flowers. This specimen says simply "California, Wallace". On the same sheet there are two other collections of Mirabilis multiflora var. pubescens. The label of one of these, W. Matthews, 1877, from Owen's Valley, is in Watson's handwriting, and he has determined the specimen to be *M*. multiflora var. pubescens. The only specimen of the Kennedy collection I have seen is at Field Museum (F), and there is no indication on the sheet that Watson saw this specimen. The label of the Palmer specimen at New York Botanical Garden (NY) is inscribed in Watson's handwriting "Mirabilis multiflora" but it is not designated var. pubescens. In addition the specimen is glabrate. I therefore designate as lectotype (GH!): California, Wallace s.n.

Oxybaphus froebelii Behr, Proc. Calif. Acad. Sci. 1:69. 1855. — Mirabilis froebelii (Behr) Greene, Bull. Calif. Acad. Sci. 1:124. 1885. — Mirabilis multiflora (Torr.) Gray var. froebelii (Behr) Jones, Contr. W. Bot. 10:49. 1902 (illegitimate superfluous name, since Jones cited

"var. pubescens Wats." as a synonym). — Quamoclidion froebelii (Behr) Standley, Contr. U. S. Natl. Herb. 12:359. 1909. Type: California, San Diego Co., "Warner's Ranch" (protologue), 1855, J. Froebel, not seen, perhaps destroyed at CAS in the fire of 1906.

Quamoclidion froebelii (Behr) Standley ssp. glabratum Standley, Contr.
U. S. Natl. Herb. 12:360. 1909. — Mirabilis froebelii (Behr) Greene var. glabratum [sic] (Standley) Jepson, Flora Calif. 1(4):458. 1914.
Type: California, San Bernardino Co., "Providence Mts.", 25 May 1902, T. Brandegee s.n. Holotype: UC!; isotype: NY!

DISTRIBUTION (Fig. 3). Northern Baja California, Mexico, through southern California, southeastern Nevada, southwestern Utah, and western Arizona, United States of America. On dry gravelly-sandy soil of mesas, washes, and open hillsides between 50 and 2100 m in Oak Woodland, Pinyon-Juniper Woodland, Chaparral, Sagebrush Scrub, Creosote Bush Scrub, and Shadscale Scrub. Flowers late April through July.

- 5c. MIRABILIS MULTIFLORA (TORT.) Gray var. GLANDULOSA (Standley) Macbr., Contr. Gray Herb. 49:49. 1917. — Quamoclidion multiflorum (Torr.) Torr. ex Gray ssp. glandulosum Standley, Contr. U. S. Natl. Herb. 12:359. 1909. Type: Colorado, "Grand Junction, dry mesa", 12 May 1894, C. Crandall 423. Holotype: US!; isotypes: MO!, NY!, RM!
- Quamoclidion multiflorum (Torr.) Torr. ex Gray ssp. obtusum Standley, Contr. U. S. Natl. Herb. 12:359. 1909.—Mirabilis multiflora (Torr.) Gray var. obtusa (Standley) Macbr., Contr. Gray Herb. 49:49. 1917. Type: Nevada, "Kernan, rocky ledges", 29 April 1902, L. Goodding 653. Holotype: RM!; isotypes: F!, GH!, MO!, NY!, POM!, UC!, US!
- Quamoclidion cordifolium Osterh., Bull. Torrey Bot. Club 55:75. 1928. Type: Colorado, Mesa Co., "six miles from Grand Junction, in the hills across the Colorado River" (protologue), "Hills across the Colorado River from Grand Junction" (label), 18 June 1926, G. Osterhout 6559. Holotype: RM!; isotypes: GH!, NY!, POM!, RM-3 sheets!

Note: two varietal names are available for this taxon, var. *obtusa* and var. *glandulosa*. The latter name has been chosen because *Crandall 423* is a more representative collection for my circumspection of the taxon, since it possesses mature fruits on some sheets while *Goodding 653* has only immature fruits.

DISTRIBUTION (Fig. 3). Scattered from Inyo Co., California, across southern Nevada and Utah to western Colorado. On gravelly-sandy soil of mesas, washes, and open hillsides between 900 and 2500 m in Sagebrush Scrub, Shadscale Scrub, and Pinyon-Juniper Woodland. Flowers May through July.

6. MIRABILIS TRIFLORA Benth., Pl. Hartw. 23. 1839. — Quamoclidion nyctagineum Choisy, in DC. Prodr. 13(2):429. 1849 (superfluous



FIG. 3. Distribution and date of collection of Mirabilis multiflora.

name). — Quamoclidion triftorum (Benth.) Standley, Contr. U. S. Natl. Herb. 12:358. 1909. Type: Jalisco, "Bolaños", 1837, T. Hartweg 197. Holotype: K!; isotypes: G-2 sheets!, GH!, P!; photographs of holotype: DS!, MICH!

Plants from taproot 1-2 m long, 2-5(-8) cm in diameter; branches ascending to nearly decumbent, 1-5 m long, forming loose trailing clumps 1-6 m in diameter, the primary branches 5-7 mm thick; herbage green, sparsely to densely glandular-pubescent, occasionally glabrate; leaves horizontally spreading, thin; lowermost leaves ovate and often asymmetrical, 3-9 cm long, 2-6 cm wide, base cordate, apex acute to attenuate; middle cauline leaves similar to lowermost leaves in all respects; uppermost leaves narrowly ovate to ovate and only slightly asymmetrical, 1-3 cm long, 0.5-1.5 cm wide, base rounded to cordate, apex acute to attenuate; petioles slender, 20-30 mm long on lowermost leaves, 5-10 mm long on uppermost leaves; leaf stomata 21-27 µm long, 15-21 µm wide; peduncles 2–15 mm long, 1 mm in diameter, erect or ascending; involucre campanulate, laterally compressed, 7–10 mm long, the bracts united by their margins, the tube 3-5 mm long, very unequally 5-lobed, the free portion of bract 3-7 mm long, 3-5 mm wide at base, triangular to very widely ovate, apex acute to attentuate; involucre 3-flowered, the flowers borne on pedicels up to 1 mm long on midvein of the two largest involucral bracts only, one flower on each midvein, the central flower solitary and naked; perianth tubular, 20-25 mm long, deep cardinal red, puberulent on both surfaces, the tube 20-25 mm long, 4-5 mm wide, a throat lacking, the five lobes very widely ovate, 1 mm long, 2.0-2.5 mm broad, apex rounded, the five longitudinal nerves extending to the sinus, apex of nerve densely pubescent; stamens exserted 7-14 mm, filaments densely pubescent, pollen grains 115–135  $\mu$ m in diameter; style exserted 7-14 mm; anthocarp ellipsodial, slightly constricted at proximal end, occasionally constricted at distal end, 4-5 mm long, 2.0-2.5 mm wide, dark brown, tuberculate, sparsely pubescent, producing copious amounts of clear mucilage when wetted.

DISTRIBUTION (Fig. 2). Scattered in scrub vegetation of Baja California del Sur and Jalisco, Mexico, occurring at 300 to 1200 m. Flowers October through April.

This is certainly the most remote taxon, both geographically and taxonomically, of subgenus Quamoclidion. Heimerl (1934) proposed that Quamoclidion be resurrected as a genus composed solely of Mirabilis triflora. He separated Quamoclidion from Mirabilis, as a genus, on the following basis: 4-lobed versus 5-lobed involucre and filaments with spreading hairs versus glabrous filaments. He further stated that only Hermidium in subtribe Mirabileae-Boerhaaviinae had similarly pubescent filaments. In fact, many taxa of Mirabilis have pubescent filaments and one of the four involucral bracts of M. triflora is deeply bifid and supplied by two vascular traces rather than the usual single midvein. Although M. triflora is quite distinctive within Quamoclidion, I prefer to keep it here until the other members of Mirabilis are better known, since I have not seen any Mirabilis that resembles M. triflora more than do plants of subgenus Quamoclidion.

## Excluded Names

Quamoclidion angulatum Choisy, in DC. Prodr., 13(2):429. 1849 (Nyctago angulata DC.; Choisy, in DC. Prodr. 13(2):429, as synonym. 1849.) Choisy doubtfully referred this species to the genus. Choisy's specimens for this taxon were collected in Mexico by Mociño and Sessé. Standley (1911) remarks that Choisy's description does not agree with the collectors' drawing of the specimen in all particulars, and Standley (1918) later concluded that "the identity of the plant is problematical." I have not been able to locate the collection made by Mociño and Sessé, but I have seen a copy of the collectors' drawing (MO). The plant represented may belong to *Mirabilis* section *Allionia*, but it is definitely not a *Quamoclidion*.

- Quamoclidion oxybaphoides Gray, Amer. J. Sci. Arts II. 15:320. 1853. ≡ MIRABILIS OXYBAPHOIDES (Gray) Gray, in Torr. Bot. Mex. Bound. Surv. 173. 1859.

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#### NOTES AND NEWS

RANUNCULUS CALIFORNICUS, A NEW RECORD FOR THE STATE OF WASHINGTON. — Known as an indicator species for coastal prairies, *Ranunculus californicus* is typically found on the islands in southern California and along the coast in northern California and southern Oregon. Until now, there were apparently only two locality records north of Lincoln County, Oregon: one disjunction from Sauvie Island, near Portland, Oregon (ORE), and one from the Trial Islands, near Victoria, British Columbia (V). Recent exploration has resulted in documentation of seven sites in the Puget Trough of Washington where *Ranunculus californicus* Bentham var. *cuneatus* Greene is locally common to abundant. All sites are open, south to southwest facing grassy bluffs or rocky slopes just above the seacoast, at elevations up to 150 feet.

Although R. californicus intergrades with  $R_{\star}$  occidentalis (L. Benson, Amer. Midl. Naturalist 40:1-261, 1948), the features demonstrated by the coastal collections from the Puget Trough are most similar to R. californicus in these diagnostic features: petals 5-14, 2-2.5 times longer than wide; nectary glands 0.5-0.8 mm long; and beaks of the achenes 0.5-1 mm long, strongly curved or hooked at the apex. Ranunculus occidentalis does occur in nearby areas but not sympatrically with R. californicus. The populations show differences in the number of petals per flower and in the proportion of petal length to width. In the populations from Fidalgo and Lopez Islands, the petals number (5-) 8-14 per flower and are typically 2-2.5 times longer than wide. On San Juan Island, the petals usually number 5-8 (-11) and are about two times longer than wide. The San Juan Island populations show greater similarity to R. occidentalis the interpopulational variation.

Specimens of *R. californicus* var. *cuneatus* from Washington, all at WTU: SAN JUAN CO. Lopez Island: Iceberg Point, 8 May 1974, *Denton 3420*, 17 Apr 1976, *Denton 3975;* Point Colville, 17 Apr 1976, *Denton 3802*. San Juan Island: west slope of Mt. Dallas, 5 May 1974, *Denton 3407*, 1 May 1976, *Elvander 602;* San Juan County Park, west side of island, 6 May 1976, *Lerner 152;* English Camp, northwest side of island, 6 May 1976, *Lerner 151.* SKAGIT CO. Fidalgo Island: Deception Pass, 17 Apr 1976, *Denton 3814;* Fidalgo Head, 17 Apr 1976, *Denton 3813.* 

I am grateful to R. E. Norris who informed me of an "unusual" buttercup on Iceberg Point of Lopez Island, to C. L. Hitchcock for verifying my identifications, and to R. L. Taylor at UBC and the curators at ORE, OSC, UBC, WS, and V for information about their collections of *R. californicus*. — MELINDA F. DENTON, Department of Botany, University of Washington, Seattle 98195.